Ocellation in *Coenonympha tullia* (MÜLLER) (Lepidoptera : Satyridae) I. Structures in correlation matrices

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Abstract

Multivariate statistical techniques (non-metric scaling, factor analysis and cluster analysis) have been used to investigate the correlation structure among spots in 914 male and 540 female *C. tullia* from the British Isles. The butterflies have been scores for six forewing and eight hindwing spots on each wing and surface (Figure 1).

Correlation structures are the same in males and females, despite the females having a greater frequency of spots in each spot position. The structures are summarized in Figure 4 : (i) Most prominent is a size factor incorporating forewing spots 1 and 4 and most hindwing spots. This has as its foci the virtually omnipresent forewing apical spot 1 and hindwing spot 5. Also individual factors occur isolating (ii) forewing spots 2 and 3 ; (iii) forewing spot a ; (iv) hindwing spots 7 and 8 and (v) hindwing upperside spots 1 and 2.

The results are considered with respect to (i) wing pattern development (ii) population comparisons on spotting and (iii) selection pressures on the wing pattern. In particular the significance of the degree of independent control by different spots and of spot foci is examined. It is held that they both form an essential part of anti-predator strategies which involves decoying strikes to least vulnerable parts of the insect (hindwing spot 5) and/or which maximally effect misses (forewing spot 1). Wing damage data corresponds with this hypothesis.

Résumé

Les auteurs ont recouru à des techniques statistiques multivariées (graduation non métrique, analyse factorielle et analyse de cluster) pour étudier la structure de corrélation entre les ocelles de 914 mâles et 540 femelles de *Coenonympha tullia* des Iles britanniques. Ces Lépidoptères sont considérés comme ayant six ocelles sur l'aile antérieure et 8 sur l'aile postérieure, et cela des deux côtés et sur les deux faces (Figure 1).

Les structures de corrélation snt les mêmes chez les mâles et les femelles, bien qu'il y ait chez les femelles une plus grande fréquence d'ocelles dans chaque position de

celles-ci. Les structures sont résumées à la Figure 4. (i) Ce qui frappe le plus est un facteur de dimension comprenant les ocelles 1 et 4 de l'aile antérieure et la plupart des ocelles de l'aile postérieure. Ce facteur a comme foci l'ocelle apical 1 de l'aile antérieure, pratiquement omniprésent, et l'ocelle 5 de l'aile postérieure. Il y a également des facteurs individuels isolant (ii) les ocelles 2 et 3 de l'aile antérieure ; (iii) l'ocelle a de l'aile antérieure ; (iv) les ocelles 7 et 8 de l'aile postérieure ; et (v) les ocelles 1 et 2 du dessus de l'aile postérieure.

Les résultats sont appréciés selon : (i) développement du dessin (pattern) des ailes, (ii) comparaison des populations quant aux ocelles et (iii) pressions de sélection sur le dessin des ailes. Est étudiée en particulier l'importance (significance) du degré de contrôle indépendant pour différents ocelles et celle des foci d'ocelles. On considère que ces deux facteurs constituent une partie essentielle des stratégies anti-prédateurs, lesquelles comprennent la déviation des agressions vers les parties moins vulnérables de l'insecte (ocelle 5 de l'aile postérieure) et/ou produisent un maximum de ratés (ocelle 1 de l'aile antérieure). Ce qu'on a enregistré quant aux dommages causés aux ailes est en accord avec cette hypothèse.

Introduction

Spotting occurs in all butterbly families but differs considerably in frequency, size, shape, position, structure and coloration from one group to the next. In the Satyridae and the underside of Lycaeninae, spotting forms a particularly important component of overall pattern. This has long attracted entomologists interested in individual variation (cf. BRIGHT and LEEDS 1938 ; LEEDS 1948 ; THOMSON 1969, 1970 ; REVELS 1975a, 1975b, 1977, 1978 ; RUSSWORM 1978). Visually-hunting predators such as birds and lizards have been assumed to provide the major selection pressures for the evolution of wing patterns and colours (POULTON 1890 ; COLLENETTE 1922) and this has been verified for a number of species (BOWERS 1980, 1981, 1983 ; BROWER 1958a, 1958b, 1958c ; BOYDEN 1976). Spot development has been interpreted as being the outcome of such pressures, their role variously described as having either a startling, confusing or deflecting function on predators (TINBERGEN 1972, 1974 ; EDMUNDS 1974 ; ROBBINS 1980). Mimicry of vital organs by spots and complementary wing attributes can be realistic as in the many Neotropical 'false head' Lycaenids (ROBBINS 1980, 1981).

Since 1946 spots have also been used as genetic markers in evolutionary studies, but with little emphasis, until recently, on their visual significance (BRAKEFIELD 1979). *Maniola jurtina* L., specifically its hindwing underside spotting, has been the most worked insect (cf., FORD 1975 ; DOWDESWELL 1981) though some geographical data have been collected for related species in the genera *Maniola* and *Pyronia* (FRAZER and WILLCOX 1975). Important variation has been disclosed within populations between

individuals and with time (intra- and inter-seasonally) and between populations (BRAKEFIELD 1979). Distinctive zones of spotting (stabilizations) gradients and sharp boundaries have been described, in depth for *M. jurtina*, but also variously for *C. tullia*, *A. hyperantus* (L.) and *P. tithonus* (L.) in Britain (DENNIS 1977) and is suspected in other species such as *E. aethiops* ESPER (THOMSON 1980). Naturally, variation in spotting extends to Satyridae elsewhere, for instance to Australian *Heteronympha merope merope* (PEARSE and MURRAY 1981, 1982) and includes other groups. Examples of British Lycaeninae are *P. icarus* ROTT. (FORD 1945) and *A. artaxerxes* Fab. (HOEGH-GULDBERG and JARVIS 1969). Elsewhere spotting and similar markings have been studied in *Acraea encedon*, Acraeidae (OWEN 1971) and in *Euphydryas editha* (Nymphalidae) (EHRLICH and MASON 1966 ; EHRLICH and EMMEL 1967, 1968).

Despite the now considerable accumulation of data on spotting in butterflies, little of this has received effective inerpretation. Heritability estimates and analysis of correlation structures, necessary explanatory prerequisites, have only recently begun to emerge for *M. jurtina* (BRAKEFIELD 1979, 1983 ; BRAKEFIELD and NOORDWIJK 1984). Substantial additive genetic variance was demonstrated for hindwing and forewing spot characters, hindwing spot heritability estimates recorded as 0.66 ± 0.11 for males and 0.89 ± 0.11 for females. With this, BRAKEFIELD has developed a model, evoking traditional concepts of visual predation, which account for sexual differentiation in spotting and clinal variation with latitude and altitude. Although there is sound argument for concentrating resources on a single species (EHRLICH et al. 1975), complementary studies on different organisms, particularly those including closed as well as open demographic units, could now well contribute to the discussion on wing ocellation.

The present paper is the first in a series on the Large Heath butterfly, *Coenonympha tullia* (MÜLLER). Marked clinal variation has long been known for the species in Britain but until recently, quantitative assays have beenlimited to the Welsh section of the distribution (TURNER 1963 ; DENNIS 1972, 1977). However, PORTER (1980) has illustrated some of the features of the cline using summary spot counts in males. Geographical variation and population associations throughout the British mainland are discussed elsewhere (DENNIS et al. in prep.). The present paper explores connections between the spot morphs with the application of multivariate techniques to correlation matrices. This approach provides a useful foundation for research into the genetics of the features. Moreover, submarginal spotting presents an extensive data system and therefore a subsidiary goal for subsequent geographical variation analysis of spotting

is data parsimony. Alternative techniques of referring to spot summaries carry with them the danger of concealing important variation for spot subsets.

A number of contrasts with *M. jurtina* make *C. tullia* an inteesting subject. The range of variation in the insect greatly exceeds *M. jurtina*, with more pronounced latitudinal and altitudinal gradients. Male *M. jurtina* have more spots than females, a relationship reversed in *C. tullia*. The emphasis in *M. jurtina* on forewing spots and costality in female spotting and hindwing spots and anality in males is not evident in *C. tullia*. Nevertheless, the ordered appearance of different forewing spots in *C. tullia*, as seen in contingency tables, and the 'correlation' of forewing and hindwing spots (TURNER 1963) implicate similar controls to those for *M. jurtina* spotting and there is every suggestion that the polygenetic frameworks for spotting in the two species are not greatly divergent. This would not altogether be unexpected. Spotting in *C. tullia* and *M. jurtina* follows the hypothetical Nymphalid groundplan of SCHWANWITSCH (1948). The border ocelli, with precise locations on the cell midrib, form a major component in the maximal wing pattern model ans it is likely, from the ubiquitous nature of spotting across many otherwise distinct taxa, that genes for the trait are of great antiquity.

Methods

Ocellation in *C. tullia* is confined to a submarginal band on both wings and surfaces. Spot positioning is related to interneural spaces and all but two spots, those between hindwing vein 1b and vein 2, occupy a single space. Two methods of spot nomenclature have been used, both referred to in Figure 1, and for the purposes of this paper we adhere to the scheme of TURNER (1963), a numerical coding initiated from the coastal margin of each wing. A maximum of six spots (a, 1 to 5) appear on the forewing and eight (1 to 8, with 6 and 7 typically proximate) on the hindwing.

Spots are quantitative as well as qualitative features. Designation of spot presence or absence can depend much on the size of the feature ; as such, significant inter-rater bias can influence coding, as shown recently for *M. jurtina* (BRAKEFIELD and DOWDESWELL 1984), when scoring is done without increased magnification. The spots comprise three components, a white pupil, often an intense silver in some individuals and populations, and a black spot which is in turn surrounded by a yellowish halo. As spots decrease in size, so too do these components, which also follow an ordered disappearance, pupillation vanishing first, subsequently the black spot and finally the halo. Much the same effect occurs with age-related insect wear. Pupillation on dorsal wing surfaces is usually poorly developed.

Ideally, the size of each spot component should be directly measured. However a simple technique has been applied in this survey which allows rapid and accurate

data retrieval (DENNIS 1972). Aspects of both development and size have been recorded for each spot and are described by four rank order states. Spot development relates to the sequence in which spot components emerge ; spot size is determined by a more arbirary threshold function ; that is, whether or not the venation on either side is touched or exceeded by the halo or black spot components (see legend to Figure 1).
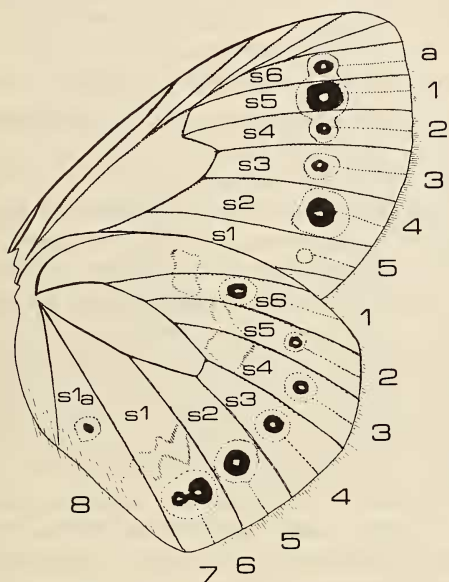

Fig. 1. Wing venation, neural space nomenclature and spot coding (Turner 1963) for *C. tullia*. Spot scoring symbols also illustrated : 0, spot absence ; x̄, halo only ; x̲, white pupil missing ; x̂, halo touches venation on either side ; ŵ, black spot touches venation on either side.
Example illustrated : a 1̂ 2̂ 3 4̂ 5̄ ; 1̂ 2 3 4 5̂ 6 7 8.
Spot scores used in the survey :

State	Spot development	Spot size
0	Absence	Absence
1	Halo only	Halo fails to touch veins
2	Halo & black spot	Halo touches or exceeds venation.
3	Halo, black spot & pupil.	Black spot touches or exceeds venation.

All observations have been carried out using a stereoscopic microscope at × 10 or × 20 magnification and the data recorded using a simple notation on cards printed with spot numbers for wings and surfaces. Care has also been taken to use direct and not transmitted light as the wings are partly transparent and underside spot features can be read in error for those on the upperside. In particular, spots on the upperside hindwing costal margin are absent though they may be well

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developed on the underside (see Fig. 1). Wing wear has been assessed using three states (none, slight, heavy) and some individuals, most affected, discounted from analyses ; moreover, pupillation is clearly influenced by insect age and wear and states 2 and 3 for spot development have thus been amalgamated. The data derive from some 30 populations covering the range of variation of the species on mainland Britain and the Scottish islands, including some 540 females and 914 males (DENNIS et al. in prep.). When sufficient numbers were available, an additional assessment of wing tear has been made on 20 specimens of each sex caught randomly from 15 populations. Detailed scoring of type (beak marks/ tear), size, position and symmetry of damage on wings has been made.

SPEARMAN's correlation as the ordinal equivalent of the Pearson product moment correlation coefficient, was selected as the most appropriate measure of association. For 2×2 tables, KENDALL's Gamma$_b$ = ø and SPEARMAN's r_s and Gamma$_b$ became increasingly similar with increasing categorization and the number of ties (DENNIS and SUNDERLAND 1979). Analyses of the connection matrices (four in all, two for each of sex and spot coding) have been effected by non-metric scaling (NMMS) algorithms, factoring and cluster techniques. NMMS and derivatives (COXON and DAVIES 1980, CARROLL and ARABIE 1980 ; CARROLL and CHANG 1970) is a technique for producing a configuration of points, usually in 2 to g-l dimensions, where g is the number of groups (five are usually sufficient) from a matrix of affinities using only information on their ranking. Starting with an initial configuration optimal geometric representations of the data are found by an iterative procedure. The configuration is modified until there is minimal distortion between distances in the space and those required to maintain the monotonicity in the original affinity matrix. The success of each subsequent iteration is measured by the stress and stress ratio. Goodness of fit measures are generally the GUTTMAN-LINGOES coefficient of alienation or KRUSKAL's stress coefficient. Naturally, negative signs are removed from correlations prior to iteration, otherwise inversely related variables would be disassociated.

Factoring techniques used include both principal components analysis and factor analysis (cf. RUMMEL 1967 ; CATTELL 1965 ; HARMAN 1967 ; MARRIOTT 1974 ; JOHNSTON 1980). Objectives are the reduction of a large number of correlated variables to some small number of functions, which are linear combinations of the original variables. Reification has been effected by matching factor loadings from a series of solutions incorporating different numbers of factors (cf., DENNIS and SUNDERLAND for details 1979). Factors have been subjected to varimax rotations which concentrate on maximizing the variance of the column loadings seeking tight clusters of variables on each vector.

Several cluster techniques to cater for extremes of behaviour in attribute fidelity have also been applied to the data, specifically single linkage, complete linkage and density analysis. Basically, the process of clustering consists of arriving at one or more partitions of a set of operational taxonomic units (in this case, attributes) each subset having more features in common than divisions obtained by any other means. All three belong to the family of sequential, agglomerative, hierarchical non-overlapping techniques (cf. SNEATH and SOKAL 1973). Procedure

density is a modification of WISHART's mode analysis (EVERITT 1974 ; WISHART 1973).

All analyses have been directed through the NUMAC IBM 370 model 168 computer under the control of the Michigan Terminal system at Newcastle University. Summary statistics, correlations and factor designs have been extracted using SPSS subprogrammes (NIE et al. 1975) ; non-metric scaling plots obtained from MDS(X) programmes (COXON 1981) and results of cluster analyses from CLUSTAN 2 (WISHART 1983).

Results and Discussion

Affinities between variables depend greatly on their frequency of occurrence. Frequency distributions for the upperside and underside spots are illustrated in Figure 2. These are much the same for males and females though it is apparent that female spotting exceeds that for the males. Spots in different positions differ markedly in their frequency and for attributes which are either ubiquitous or rare, correlations will be reduced inasmuch as variation will be limited. Such are the omnipresent apical spot on the forewing, hindwing spot 5, and the rare forewing spot 5 and hindwing spot 8. Forewing ocellation focuses on the apical spot 1 and to a lesser extent spot 4 ; whilst hindwing spotting pivots around spot 5 and secondarily spot 1. Parallel development occurs on the upperside and underside, though upperside spotting is less common and in effect mirrors underside morphological development. However, marginal spots differ markedly in frequency on the hindwing upperside and underside, more especially the costal spotting, 1 and 2, on the upperside. Much greater variation is available using the spot size criterion, as the forewing apical spot and hindwing underside spot 5 attain maximum development commonly only in lowland English populations.

The highest correlations, not surprisingly, are for bilateral homologues (ie., between spot positions on the same wing and surface but different sides of the body). As such, values for those have been amalgamated. Histograms for the remaining $n(n-1)/2$ coefficients, in which the data for sexes have been lumped, are illustrated in Figure 3. In drawing up the histograms, signs for correlations have been removed, but negative affinities are few and not significantly different from zero (maximum for spot size, -0.014 ; maximum for spot development, -0.023). The distributions are positively skewed with a tendency to bimodality, and average values reflect the modest size of most affinities. Very clearly, the spot size measurement produces higher correlations than spot development.
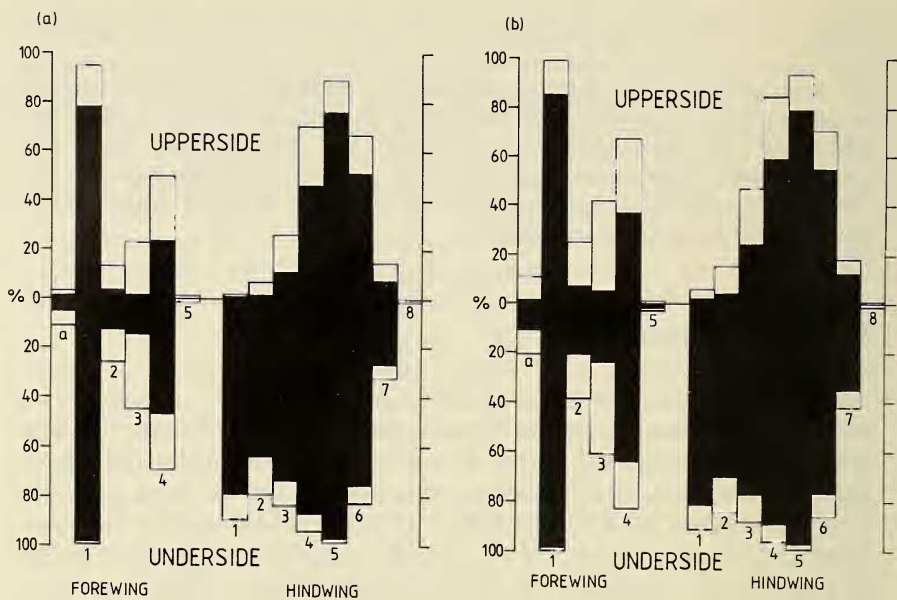
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Fig. 2. Frequency distributions for individual upperside and underside spots in (a) male (N = 914) and (b) female (n = 540) *C. tullia*.

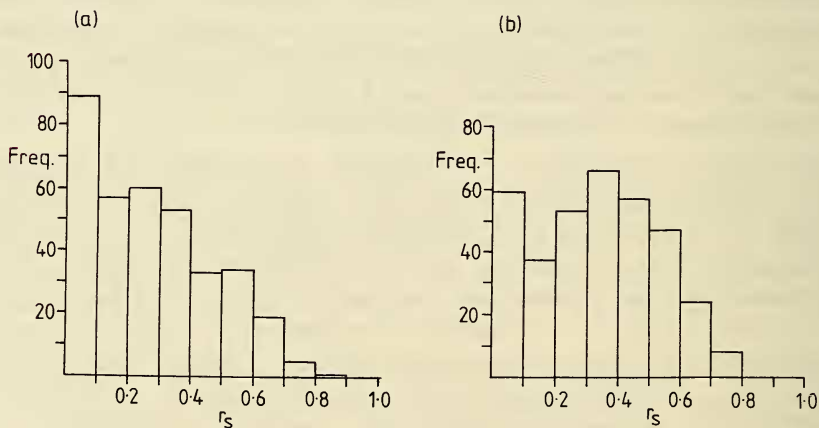Fig. 3. Frequency distributions for correlations (r$_s$) between individual spots on the upperside and underside. Data for sexes and for corresponding spots on different sides of the body have been amalgamated. (a) spot development ; (b) spot size.
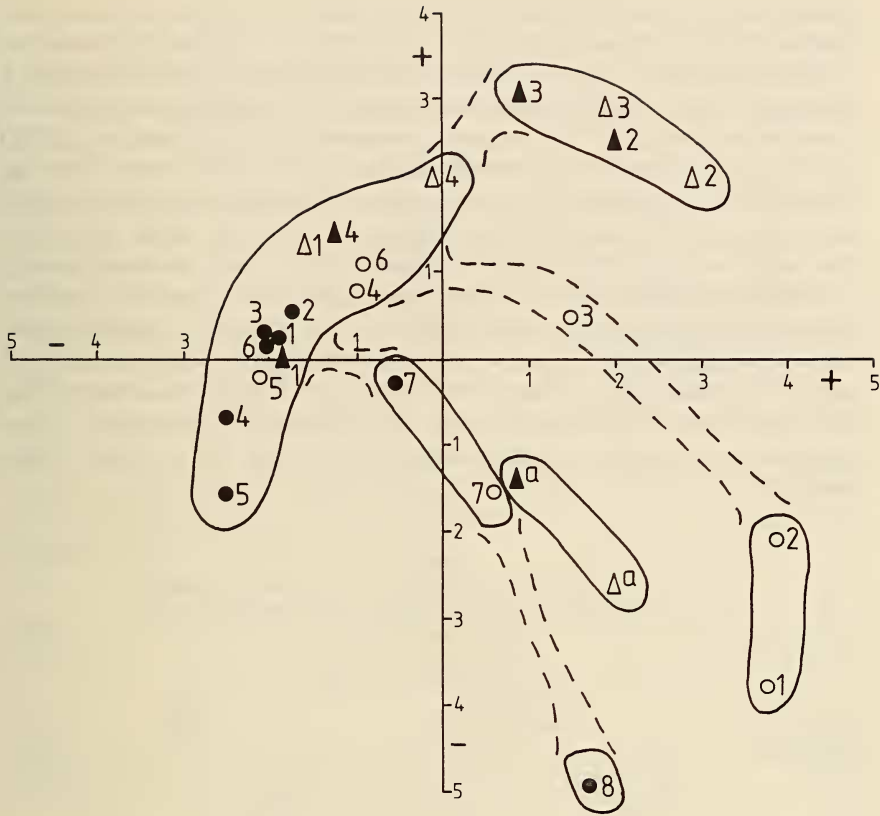
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Fig. 4. Summary INDSCAL-S plot from four NMMS analyses of male and female data for individual spots coded for development and size. Triangles, forewing spots ; circles, hindwing spots ; open symbols, upperside ; black symbols, underside. Envelopes represent entities identified from a series of varimax factor solutions.

Dimensionality	average stress	Random stress
3	0.0712	0.2491
2	0.1159	0.2816
1	0.2237	0.5036

Non-metric scaling plots (dimensions = 2 to 5) have been produced for both variable suites and separate sexes. Solutions are very similar and all stress values for the plots very low compared to random arrays of points. Forewing spot 5 and hindwing upperside spot 8, influenced by their low frequencies, occur as outliers in the plots and have been removed so that the remaining attributes can be examined at higher resolution. Figure 4 illustrates the summary INDSCAL-S product together with average stress

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values for each NMMS plot. The comparison of stress coefficients with random rankings stress values show these to be an accurate representation of spot affinities (cf., SPENCE 1979). Most attributes are contained within a compact but drawn out envelope extending from hindwing underside 5 to forewing upperside 4. This mostly comprises hindwing features, all but spots 7 and 8 from the underside but only spots 4, 5 and 6 from the upperside. Forewing spots 1 and 4 are part of this unit. As separate entities and suggestive of some independence are forewing spots 2 and 3 ; forewing spot a ; hinding upperside spots 1 and 2 ; and hindwing spots 1 and 8. Despite this, most of these groupe tie up with the main batch of variables in an ordered manner. Thus, the sequences of : − forewing spots 2, 3 and 4 ; hindwing upperside 1, 2, 3 and 4 and hindwing underside 6, 7 and 8. Forewing spot a is more difficult to place. Most noticeable in all the plots are the comparatively weak ties between corresponding spot positions on separate surfaces compared to spots on the same wing surface.

Table 1
Principle components, eigenvalues and variance estimates
for 28 *C. tullia* spot morphs scored for development and size
(sexes amalgamated)

| Component Extracted | *C. tullia* Spot Variables | | Spot Size | |
| | Spot Development | | | |
	Eigenvalue	% Variation	Eigenvalue	% Variation
1	9.281	33.1	10.852	38.8
2	2.999	10.7	2.082	7.4
3	1.395	5.0	1.506	5.4
4	1.339	4.8	1.231	4.4
5	1.203	4.3	1.189	4.2
6	1.167	4.2	1.058	3.8
7	1.052	3.8	0.993	3.5

Eigenvalues and variances for the first 7 principal components are given in Table 1. Apart from the first 2 functions only small increments in variance are provided by subsequent vectors, some 12 to account for 80 % of the variance (Figure 5). Taken together with the modest contribution of the first vector, typically a size component, numerous controls (unique factors) each having a small effect are implicated. No differences were found in the distribution of loadings on preliminary examinations of data for the separate sexes. Thus 11 to 4 factors have been extracted in repeated runs with data for sexes amalgamated. This technique results in

absorption of specific factors as the number of vectors is reduced. Typically, forewing 4, hindwing 8, hindwing 7, forewing 5 (upperside) are lost first from factoring of both variable suites. Close identity occurs for the remaining vectors, these summarized in Table 2, and recall the IDSCAL-S product ; a size factor focusing on hindwing spotting and forewing spots 1 and 4 ; and separate factors for forewing spots 2 and 3, forewing a, hindwing upperside 1 and 2 and to a lesser extent forewing 5 and hindwing 7 and 8. Factoring of both variable suites also points to substructures in the size factor, a tendency for upprside and underside spotting to diverge. This division is clearer for spot size, fusion occurring with 6 factors. However, for spot development, forewing underside spots 1 and hindwing underside spot 5, as the smaller subunit, remain isolated throughout. As alluded to above, this is likely the result of limited variation for these spots which are virtually intact in all specimens. As such they form the focus for the size factor. The pattern of coefficient weightings highlight the distribution of loadings for variables and these are illustrated in Figure 6 for the first 6 factors ; this equates well with the eigenvalue cutoff of unity.
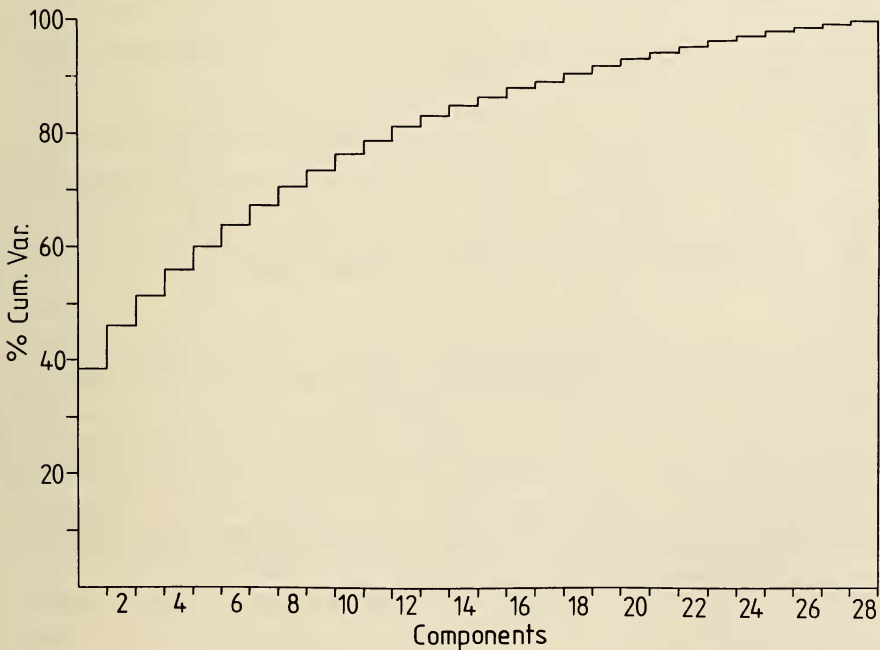

Fig. 5. Cumulative variance for sequentially extracted components of 28 spot development variables. Data for sexes amalgamated.

Table 2
A summary of recurring factors ($N_F = 6$) for 28 *C. tullia* spot morphs
(FW, forewing ; HW, hindwing ; UP, upperside ; UN, underside)

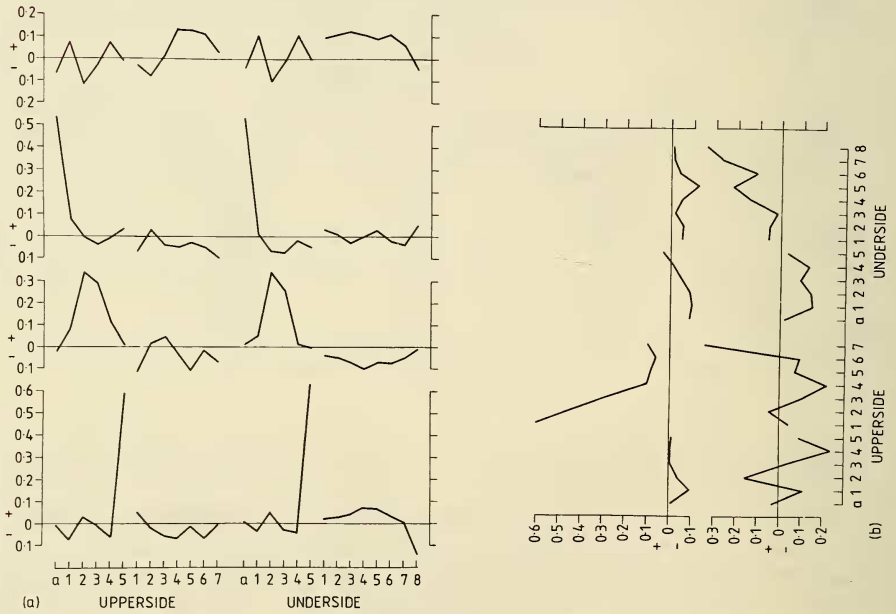| Factors	Spot Development	Spot Size
1	SIZE FACTOR	SIZE FACTOR
	HW UN 1-6 (7)	HW UN 1-6 (7)
	HW UP 3-6 (7)	HW UP 3-6 (7)
	FW UP and UN 1 and 4	FW UP and UN 1, 3 and 4
	(FW UN 1 and HW UN 5	
	remain separate)	
2	FW UP and UN a	FW UP and UN a
3	FW UP and UN 2 and 3	FW UP and UN 2 and 3
4	HW UP 1 and 2	HW UP 1 and 2
5	FW UP and UN 5	FW UP and UN 5
6	HW UN 8 (UP 8)	HW UN 7 and 8 and UP 7 (8)

Fig. 6. Coefficient weightings over individual spots for 6 factors (spot development). (a) size factor and factors for forewing spots 1, 2 and 3, and 5 respectively ; (b) factors for hindwing upperside 1 and 2, and hindwing 7 and 8. Data for sexes amalgamated.

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Much the same end products are determined by cluster analysis. The size component emerges in all routines, a linear product, very much as suggested by NMMS and factoring, emphasized in attribute chaining and the stair-like dendrograms. There is a hint too of the upperside and underside subunits in the size factor. Procedure density isolated two definitive structures apart from the size factor ; for forewing spots 2 and 3, and for forewing spot a respectively, corroborating the results of previous analyses. Hindwing upperside spots 1 and 2 ; hindwing spot 7 and forewing spot 5 are absorbed into the size factor but hindwing spot 8, and to a lesser extent forewing 4, retain considerable independence.

The various relationships expressed by three analytic techniques are summarized in the IDSCAL-S plot in Figure 4 ; envelopes have been drawn around related variables but it is not suggested that all have the same biological significance. For instance, forewing 5 and hindwing uppersides 1, 2 and 7 are distinguished more by their absence than by affinity profiles ; a similar argument may involve hindwing 8 which nevertheless does vary independently from other hindwing spots. This can be readily confirmed by its moderate frequencies at Meathop and its extreme rarity in Whixhall, Delamere and Pilling samples, despite overall spot size and development being very much of the same order throughout these populations. It follows largely that hindwing upperside 3 and hindwing 7 are drawn out of the size factor by these attributes. Nevertheless, what is surprising is the degree of independence of spot 7 from spot 6 considering they are proximate and share an interneural space. A degree of biological independence from the general ocellation, therefore, can be argued for several units : − those which straddle the apical eyespot, notably forewing spots a and spots 2 and 3, and hindwing spots 7 and 8, all of which vary substantially in frequency from one population to the next.

Some comparison can be made with *M. jurtina* but only for groups of spots. In studying these, BRAKEFIELD (1979) has provided some direct measurements but has amalgamated details for individual spots on the hindwing underside, necessary for features occurring at low frequency in small samples. Eight attributes are involved : the area of the forewing upperside and underside apical spot area and of their pupillation ; measurements of forewing upperside and underside apical spot bipupilla-tion and of hindwing spot number and area. Non-metric scaling and cluster analysis have been carried out on the male and female correlation matrices (DENNIS unpub. material).

On the whole, there are much stronger ties between spot homologues on different forewing surfaces than in *C. tullia*, but this likely reflects more

the use of precise measurements than a threshold function applied herein. The opposite may well be the case for the hindwing, as in *M. jurtina* upperside hindwing spotting is most unusual (ie., referred to as f. *postexcessa* LEEDS by entomologists (THOMSON 1969)). A close relationship occurs between attribute states for the apical spot in *M. jurtina*, more so between pupillation and spot area (r, 0.468 to 0.655) than either of these with bipupillation (r, 0.196 to 0.441). Hindwing spot number and area are also very closely related (r, 0.706 to 0.828). Increased spotting on the forewing in *C. tullia* is achieved by additional spotting rather than by bipupillation (effectively the expansion of the apical spot into the adjacent interneural space), and these spots (a, 2 and 3) retain substantial independence. However, from casual observations, pupillation and number of spots in *C. tullia* increase with average spot size. Weakest correlations in *M. jurtina* (r, 0.096 to 0.514) exist between hindwing and forewing attributes, though correlations between forewing and hindwing underside are higher than between forewing and hindwing upperside, much as in *C. tullia*. The implication is of greater interdependence in forewing and hindwing spotting (involving specifically those spots forming part of the size factor) in *C. tullia* than in *M. jurtina* but additional information is required.

Both *C. tullia* and *M. jurtina*, indeed all the Satyridae, have in common much reduced combinations of spotting than expected from 2^n, where n is the number of spot positions, the individual terms of the binomial expansion. In *M. jurtina* only some 13 spotting morphs occur of the expected 64 and a number of these are uncommon. In *C. tullia* similar limitations have been illustrated in spot polychotomies by TURNER (1963) and DENNIS (1972). As we have seen, such combinations reflect degrees of dependence and interdependence between individual spots and a hierarchical structuring in spot development, which corresponds much with the relative size of spots in different positions. This is also influenced by sex in both species, in *C. tullia* the effect probably being to increase spot apparency (size) and thus spot number.

These results contribute to three related areas of research : − to the construction of models of wing pattern development and of genetic controls, to investigations of potential selection pressures and to analyses of interpopulation affinities. Correlations between spots and subsidiary attribute states provide specific data for examining the appropriateness of alleged components in wing pattern models, such as 'standing waves', 'diffusion cones' and 'planes of interpretation' (cf., MAYNARD-SMITH 1968 ; WIGGLESWORTH 1972 and NIJHOUT 1978). These ideas have recently been applied to *L. bellargus* (ROTT.) (Lycaenidae) with some degree of success (ROBERTSON and YOUNG, 1982).

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The evolution of spotting in insects although long attributed to visual selection by predators has only recently been formulated for *M. jurtina* by BRAKEFIELD (1979). Previously, the rather insignificant hindwing spotting in *M. jurtina* was explained by pleiotropy and as the outcome of mostly unknown factors operating in early stadia, especially during the larval stage (cf., DOWDESWELL 1961). Certainly, ocellation in *C. tullia* is sufficiently striking to be apparent to potential predators, and from this vantage alone data regarding spot covariation are important. Moreover, distinctions between spots having a startling, confusing or deflecting function on predators are closely associated and highly relevant. To a large extent, a degree of independence between spots in different positions is expected, as the positions are not only relative to one another but also to vital organs. Strikes by predators at some spots from particular angles would have a greater likelihood of inflicting critical damage than at others, and in a highly integrated system involving spots of similar size and apparency, protection gained, therefore, from an increase in some spot features could lead to greater vulnerability from a concomitant increase in others. Thus successful attacks launched by predators and the hindwing anal margin (spots 4 and 5) would likely result in wing tear and escape, but strikes directed to the costal area of the hindwing could pin all 4 wings of a resting insect together and give the predator a second chance.

The apparency and extensive development of spotting in *C. tullia* over both wings, as well as the relatively high degree of coordination of the spot morphs (almost certainly underestimated herein compared to spot measurement) suggests a multiple protection system, predators not only being confused by the array of 'eyes' seen while the insect is on the wing or at rest, but then being deflected towards the largest and brightest spots and spot areas in the least vulnerable positions, the apical spot and hindwing spots 4 and 5, which allow the insect to escape minus a portion of the wing. Data in Table 3 show this to be largely true, the assumption being of course that wing tear results from predator strikes (DENNIS in prep.). Apart from the exception perhaps of hindwing spot 1, wing tear corresponds closely with the frequency and size of spots in different positions. Thus, strike counts at forewing spots 1 and 4 and hindwing spots 4, 5 and 6/7 relate to their apparency and occurrence, as does the lack of tear where spots are absent. Exceptions too are not without logical explanation. Relating strikes to spots does make the additional assumption that attacks are accurate. Misses evidently occur inasmuch as tears are frequently found between spots and often fall short of them. The lower frequency of tears over hindwing spot 1 may result from its placement deeper into the wing ; moreover, damage regularly occurs in interneural space 5 despite the virtual absence of spot 2. There is evidently less

damage over the forewing apical spot than may be expected from its prominence. This likely reflects the function of the spot, particularly its capacity to startle, as well as the conditions of predator strikes, which we believe are more common while the insect is at rest and the forewings are concealed. It may also point to the greater importance of the forewings to the butterfly which is further implied by their larger surface area and thickened costal margin. Some attacks at the apical spot have been launched from the front and such costal margin strikes could be particularly disadvantageous as a broken forewing reduces flight efficiency more than other types of wing damage. However, forewings in resting *C. tullia* are usually well-protected inasmuch as the insect once alerted, explosively thrusts its forewings forward out of the main target area presented by the hindwing spotting. Small birds seem incapable of breaking the forewing costal margin; one Thorne Waste male had experienced seven pecks each of which had left only an impression across the forewing costal margin. If caught by all four wings, then the forewings are contained within an envelop of hindwings and the insect has a further chance to escape as the predator attempts to grasp the body area. The full implications of the wing tear date are explored in a separate paper (DENNIS in prep.).

Table 3

Frequency distribution of beak impressions and tears on the wings of 301 male and 284 female *C. tullia* from 15 populations. Multiple classification of damage to spot positions has been used in cases where strikes have effected more than one spot. CM = costal margin; IM = inner margin; numbers refer to spot positions on the outer margin.

	MALES			FEMALES		
FOREWING	Small Tear	Large Tear	Total	Small Tear	Large Tear	Total
CM	1	3	4	2	11	13
CM1	3	2	5	5	5	10
a,1	34	13	47	26	5	31
2	7	4	11	4	2	6
3	16	2	18	8	3	11
4	16	7	23	9	5	14
IM5	7	5	12	4	3	7
HINDWING						
CM	2	4	6	0	6	6
CM1	0	1	1	0	2	2
1	6	6	12	6	11	17
2	10	10	20	7	17	24
3	14	12	26	14	11	25
4	22	21	43	19	14	33
5	29	29	58	22	20	42
6,7	17	29	46	11	22	33
IM8	5	3	8	2	3	5

Increased female spotting and decreased spotting with latitude (PORTER 1980) and altitude (DENNIS 1977) implicate behavioral and environmental differences respectively. Part of the explanation lies in the selection for crypsis in conditions discouraging activity, bearing in mind that bright spots can attract as well as repel predators. BRAKEFIELD (1979) has ably explained the conflicting nature of selection for increased and decreased spotting on different wings for the sexes separately in *M. jurtina* on this basis. Regarding *C. tullia*, differences between populations and the sexes are examined elsewhere (DENNIS *et al.* in prep.).

Some compromise in population studies is required between examining variation for individual spots separately, and compounding data in spot counts ovr wings and surfaces. The former is repetitive, fruitless and wasteful of effort and the latter often conceals important population differences between separate morphs by averaging out distinctions. At very least, the correlation structures provide a realistic framework for investigating interpopulation variability ; idiosyncratic population features await explanation such as the greatly elevated frequencies of hindwing spot 8 in coastal Westmorland and the very low levels of forewing spot 2 at Whixhall in Shropshire. However, despite the limited status of the size factor, accounting for perhaps less than 38 % of the total variance, independent spot factors and cumulatively large unique variance do not preclude correlation between populations for separate spot vectors, and summary counts can still usefully be employed in spatial designs. Nevertheless, interpopulation affinities will best be served by multivariate techniques.

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